NEANTHES (POLYCHAETA: NEREIDIDAE) FROM VICTORIA WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: Two nereidid polychaetes are described from Victoria, *Neanthes bassi* sp. nov, and *N. flindersi* sp. nov, *Neanthes succinea* Leuekart is recorded from Australia for the first time and the status of *Nectoneanthes* Imajima is discussed. A systematic account of *Neanthes* known from Victoria and a key to species recorded from southern Australia are provided. A list is appended of all species of *Neanthes* described to date.

During the years 1979-1983 the Museum of Victoria (previously National Museum of Victoria) made extensive collections of soft bottom benthos as part of a survey of the marine fauna of Bass Strait. This paper reports on nereidid polychaetes of the genus *Neanthes* collected during that survey and on additional material from other collections deposited in the Museum of Victoria.

MATERIALS AND METHODS

Locality data for all stations occupied during the Bass Strait Survey (BSS prefixcs) are being published elscwhere (Wilson & Poore in prcss) and complete localities are only given here for type specimens. Sources for other collections included in this study are: the Port Phillip Bay Environmental Study (PPBES) (Poore *et al.* 1975, Poore & Kudenov 1978); littoral and benthic surveys of Western Port (Smith *et al.* 1975); Crib Point Benthic Survey (CPBS) and Westernport Bay Environmental Study (WBES) (Ministry for Conservation 1975, Coleman *et al.* 1978); Gippsland Region Environmental Study (GRES) (Poore 1982); N.S.W. Shelf Benthic Survey (SBS) (Jones 1977).

Registration numbers of Museum of Victoria material arc prefixed NMV. Paratypes have been deposited at the Australian Museum, Sydney (AMW or AME, Endeavour material), British Museum (Natural History), London (BMNH) and the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM). Zoologisches Institut and Zoologisches Museum der Universität Hamburg is abbreviated to HZM and Western Australian Museum (Perth) is abbreviated to WAM.

The Australian distribution of each species is taken from Hutchings and Turvey (1982) and full Australian synonomies can be found in Day and Hutchings (1979). A key is provided to all species of *Neanthes* known from Victoria, Tasmania, South Australia and Western Australia south of Perth (32°S). All species have been recorded from Victoria and Bass Strait with the exception of *Neanthes isolata* Hutchings & Turvey 1982 which is known only from South Australia (Hutchings & Turvey 1982) and is not treated in the systematic text.

Diagnosis of species of *Neanthes* rely heavily on the number and arrangement of paragnaths on the pharynx, particularly on the oral ring and on the relative propor-

tions of the parapodial lobes, particularly on posterior setigers. In this study the distribution along the body of two types of neuropodial setae, heterogomph spinigers and heterogomph falcigers was found to provide useful additional characters with which to distinguish species. This information is presented for new and previously described species and is also used in the key to species. Identifying patterns in setal distribution requires location of the exact position at which a change occurs (e.g. the setiger at which heterogomph falcigers first occur). Preliminary investigations indicate that differences between left and right of the same setiger are not significant and where possible right side parapodia were examined for this study. Body width measurements given refer to width excluding parapodia.

KEY TO SPECIES OF *NEANTHES* FROM SOUTHERN AUSTRALIA

- Notopodia with three approximately equal lobes throughout (median lobes may be reduced on posterior setigers of small specimens)2 Notopodia with two lobes (small presetal lobe may be present anteriorly, usually setigers 10-20)3
- 2. Oral ring paragnaths (Areas V-VIII) a continuous band 2-5 deep; Area I with more than 10 cones *Neanthes cricognatha* Oral ring paragnaths a centrally isolated group of up to 12 on VI, a broad band tapering to 1 row laterally on VII-VIII; Area I with fewer than 10 cones *Neanthes succinea*
- 3. Area VI without paragnaths or with an isolated central group of paragnaths4 Area VI with a transverse row of paragnaths8
- 5. Area III with about 20 paragnaths or more, V with 3 in a triangle (rarely I or 2 but never in longitudinal series); specimens wider than 1 mm with presetal lobe in anterior notopodia, usually first 6-20 setigers (lives intertidally on sheltered coasts) Neanthes vaalii

Area III with 8-16 paragnaths, V with 3-6 including 2-3 in longitudinal series; presetal notopodial lobe absent on all specimens up to at least 2 mm width (lives intertidally on exposed coasts) *Neanthes isolata*.

- 7. Area VI with 0-1, VII-VIII with 0-6 paragnaths Neanthes kergnelensis Area VI with 1-3, VII-VIII with 16-30 paragnathsNeanthes flindersi sp. nov.
- 8. Area VI with a single transverse row of larger paragnaths and occasional smaller ones, VII-VIII with mainly large cones, usually fewer than 50Neanthes uniseriata Area VI with 2 rows of large cones and a variable row of smaller cones, VII-VIII with large and small cones, usually more than 50Neanthes biseriata

SYSTEMATICS

Genus Neanthes Kinberg 1866

DIAGNOSIS: Eversible pharynx with conical paragnaths on both rings. Four pairs of tentacular cirri, parapodia biramous. Notosetae homogomph spinigers; neurosetae homogomph and heterogomph spinigers and heterogomph falcigers (after Fauchald 1977a).

TYPE SPECIES: N. vaalii Kinberg 1866

SPECIES INCLUDED: See Appendix.

Neanthes bassi sp. nov. Fig. 1

1971 *Platynereis australis* Schmarda; Knox & Cameron, p. 28. (*partim*)

MATERIAL: Holotype, NMVF50005 Bass Strait, N of Robbins Island, NW Tasmania (40°31'S, 144°56'E), 27 m very coarse shell, epibenthic sled, P. Forsyth et al. on F. V. Sarda, 2 Nov. 1980 (Stn BSS 109). Paratypes, NMVF50006-9, AMW198701-2, BMNHZB 1984, 47-48, USNM097289, 097280 all from type locality; Bass Strait, N of Robbins Island NW Tasmania (40°31'S, 145°04'E) 29 m, sand (Stn BSS 111 SEB), NMVF50010; Bass Strait, NE of Robbins Island, NW Tasmania (40°22'S, 145°17E 40 m, sand (Stn BSS 112 SEB), NMVF50011. Additional Material, Bass Strait, E of Corner Inlet, (Stn BSS 178 TAM), NMVF50012-F50016; Bass Strait, S of Orbost, (Stn BSS 207 SEB), NMVF50017; Port Phillip Bay Survey Arca 9 Stn 178, NMVF50123 (2 specimens); Port Phillip Bay Survey Area 55 Stn 148, NMVG1866 (part of material identified as *Platynereis australis* Schmarda 1861 by Knox & Cameron 1971).

Unpublished notes from the Port Phillip Bay Environmental Study (1969-1973) indicate that *Neanthes* sp. I, species no. 471, PPBES Stn 984, I specimen and nereid sp. 2, species no. 690, PPBES Stn 928, 2 specimens (Poore *et al.* 1975, p. 50) may represent additional record(s) of *Neanthes bassi* sp. nov. However these specimens appear to have been lost.

DESCRIPTION: Holotype an anterior fragment of 36 setigers, 8 mm length, 1.5 mm maximum width. Colour in alcohol pale brown with darker brown pigmentation on prostomium and darker brown transverse bands on dorsum of apodous segment and first setiger. Prostomial length slightly exceeds width. Two pairs of eyes, pigmentation lost. One pair of stout palps with small globular palpostyles, one pair of antennae approximately equal in length to prostomium. Four pairs of tentacular cirri, faintly annulated, longest extending to setiger 4. Jaws large, translucent brown with 6 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area IV only, arranged as follows: I = 1; II = 13, 15 in two crescent shaped rows; III = 6 in a single transverse row; IV = a triangle of 7 cones and also a triangle of 5 smooth bars; V = 1; VI = 8, 6 in a roughly circular patch; VII-VIII = 9 in a single row.

Notopodia with two approximately equal lobes, presetal notopodial lobe absent, dorsal cirrus of approximately equal length to notopodial lobes, becoming approximately 1.3 times longer on posterior setigers. Notopodia becoming elongate, approximately 1.5 times longer than neuropodia on posterior setigers. Neuropodia bilobed, lobes approximately equal on anterior setigers, ventral lobe becoming reduced posteriorly, neuropodial digitiform postsetal process present on setigers 1-6. Ventral cirrus basally attached, approximately half length of neuropodium throughout (Fig. 1b, c). Notosetae homogomph spinigers from setiger 3 (setigers 1 and 2 uniramous). Dorsal fascicle of neurosetae include homogomph and heterogomph spinigers on setigers 1-5, joined by heterogomph falcigers (Fig. 1d, e) from setiger 7. Ventral fascicle of neurosetae include heterogomph spinigers only, on anterior setigers, plus heterogomph falcigers from setiger 7.

VARIATION: Variations not described for the holotype based on 11 paratypes (anterior fragments, size range 14 setigers, 3 mm length, less than 1 mm width, to 35 setigers, 17 mm length, 3 mm width) and on additional material listed above (largest specimen entire, 106 setigers, 51 mm length, 3 mm width, NMVG1688). Dorsum of a variable number of anterior setigers often with a pair of dark brown patches. Antennae equal to or slightly exceeding length of prostomium. Tentacular cirri faintly annulated, longest extending to setiger 4-9. Pharynx with conical paragnaths on both rings and smooth bars also present on Arca IV only, arranged as follows: I = 0.1 (rarely 2 or 3 in longitudinal series); II = 6-27 in two crescent shaped rows; III = I-I3; IV = atriangle of 3-18 cones and also a triangle of 3-7 smooth bars (Fig. 1a); V = 0-I; VI = 2-9 in a roughly circular patch; VII-VIII = 5-29 in 1-2 rows decreasing laterally.

NEANTHES (POLYCHAETA:NEREIDIDAE) FROM VICTORIA

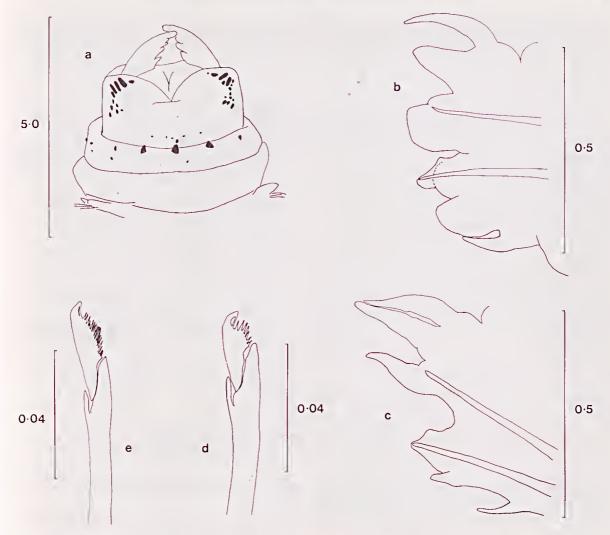


Fig. 1 – Neanthes bassi sp. nov. a, ventral view of everted pharynx (paratype NMVF50006). b, anterior view of 10th parapodium (holotype NMVF50005). c, anterior view of 32nd parapodium (holotype NMVF50005). d, ventral neuropodial heterogomph falciger, setiger 10 (holotype NMVF50005). e, ventral neuropodial heterogomph falciger, setiger 32 (holotype NMVF50005). Scales in mm.

Specimens exceeding about 1 mm body width with neuropodial digitiform postsetal process on anterior 5-10 setigers. Heterogomph falcigers appear in dorsal neuropodial fascicle from setigers 4-6 and in ventral neuropodial fascicle from setigers 4-7. One specimen, NMVF50014, has heterogomph falcigers present in the neuropodium at setiger 2. However in all other respects this specimen agrees with the description given here. Heterogomph spinigers are present in both neuropodial fascicles from setiger 1 but are replaced posteriorly by homogomph spinigers. Homogomph spinigers do not appear before setiger 7-8 and heterogomph spinigers persist as 1-2 setae in the dorsal region of the ventral neuropodial fascicle back to setigers 12-40.

Anal cirri extend back 17-25 setigers on the only two specimens which are complete posteriorly (NMVG1688).

No specimen examined has obvious coelomic gametes.

REMARKS: Fauchald (1972) subdivided *Neanthes* on the presence or absence of falcigers and on the relative development of parapodial lobes. *Neanthes bassi* belongs to his Group IIB 1 with notopodial lobes approximately equal in size and of similar relative proportions posteriorly. Within this group 12 species are similar to *N. bassi* in that paragnath counts include a group of fewer than 20 on Area III, a roughly circular group on VI and a band of 1-2 rows on VII-VIII. *Neanthes (Hediste) diversicolor* (Müller 1776), *N. limnicola* (Johnson 1903), *N. japonica* Izuka 1908 and *N. unifasciata* (Willey 1905) are all estuarine forms and can be distinguished from *N. bassi* by their fused simple falcigers in the posterior neuropodia. The remaining 8

	Area I	Area 111	Area V	Area VI	Area V11-V111	Presetal (3rd) notopodial lobe (anterior	Postsetal (3rd) neuropodial lobe setigers)	Source of data
N. bassi sp. nov.	0-3 (LS)	1-13	0-1	2-9	5-29 (1-2 R)	absent	present	this study
<i>N. flava</i> Wu Baoling & Sun Ruiping 1981	1	1	0	6-7	40-60	present	absent	Wu Baoling & Sun Ruiping 1981
<i>N. galetae</i> Fauchald 1977b	2	18	0	8	5 (1 R)	absent	present	Fauchald 1977b
N. indica brunnea Day 1957	2-3 (LS)	7-10	0	6	2-3 R	present	present	Day 1957
N. isolata Hutchings & Turvey 1982	1-2 (LS)	8-12	3-6	6-11	37-55 (2-3 R)	present	absent	Hutchings & Turvey 1982
N. macrocephala Hansen 1882	2 (LS)	13	2 (1 R)	7	2-3 R	not recorded	not recorded	Hansen 1882
<i>N. nanhaiensis</i> Wu Baoling & Sun Ruiping 1981	0-1	1-5	0	0-2	1-4 (1 R)	present	present	Wu Baoling & Sun Ruiping 1981
<i>N. vaalii</i> Kinberg 1866	1-4 (LS)	19-28	1-3	3-5	37-59 (2-3 R)	present	absent	this study
N, virens (Sars 1835)	0-7	4-14 (2-3 R)	0-4	0-5	2-3 R	present	present	Pettibone 1963

TABLE 1 Neanthes Group 11B 1 (part; emended after Fauchald 1972). Comparison of species lacking fused falcigers, with fewer than 20 paragnaths on Area 111, with a circular group on Area V1 and a band of 1-3 rows on Areas V11-V111.

Explanation of abbreviations: $\times R = \times$ transverse rows of paragnaths; LS = in longitudinal series.

species can be distinguished from *N. bassi* using the characteristics given in Table 1. In this study, *N. virens* (Sars 1835), has been moved from Group I to Group IIB 1. See Remarks under *N. succinea*, below.

Among the species of *Neanthes* known to occur in southern Australia, *N. bassi* most closely resembles *N. vaalii* Kinberg 1866. However, the two species differ not only as shown in Table 1 but also in the distribution of neurosetae: *N. bassi* lacks heterogomph falcigers on a variable number of anterior setigers and lacks heterogomph spinigers on a variable number of posterior setigers in contrast with *N. vaalii* in which both heterogomph spinigers and falcigers are present in all neuropodia.

Neanthes bassi also appears to differ from all species presently described for the genus in the degree of development of bar shaped paragnaths on Area IV. The presence of paragnaths with transversely elongated bases along with cones was noted on Area IV of *N. nanciae* (Day 1949, p. 445) and in the course of the present study bar paragnaths were noted on Area IV of *N. isolata* Hutchings & Turvey 1982, *N. vaalii*, *N. biseriata* Hutchings & Turvey 1982, and *N. uniseriata* Hutchings & Turvey 1982. In each case bars are situated close to the base of the maxillae but in no other species are they developed to the extent that they equal or exceed the area occupied by cones on Area IV as in *N. bassi* (Fig. 1a).

ETYMOLOGY: *Neanthes bassi* is named after George Bass, who first navigated Bass Strait.

DISTRIBUTION: Southwestern and northeastern Bass Strait and Port Phillip Bay, Victoria. Known only from southeastern Australia.

HABITAT: Various sand shell and mud sediments, 7-51 m.

Neanthes cf. N. bassi sp. nov.

MATERIAL EXAMINED: Stn BSS 170 GSM, NMVF50018; Stn BSS 170 SEB, NMVF50019-F50021.

REMARKS: Four specimens from Stn BSS 170 in eastern Bass Strait appear to be closely allied to N. bassi but their identification must remain doubtful until more material is available. These specimens differ from N. bassi as shown in Table 2.

Neanthes biseriata Hutchings & Turvey 1982

1982 Neanthes biseriata Hutchings & Turvey, p. 108, fig. 6a-e, table 6.

MATERIAL EXAMINED: W.A.-Emu Point, Albany, coll. 6 Jan. 1973, WAM79-74 (includes 1 immature female epitoke).

S.A. – Speeds Point, Streaky Bay (04A), 4 paratypes, AMW18423; Venus Bay (06B), 40 paratypes, AMW18418; Victor Harbour (18A), 46 paratypes, AMW18420; Encounter Bay coll. 3 Jan. 1977, AMW194928 (full locality data given by Hutchings & Turvey 1982).

Tas.-Goose Island, coll. 20 Jan. 1979, NMVF50130. Vic.-Kilcunda, coll. Jan. 1966, NMVF50061, F50063, F50065; Somers, Western Port, NMVF50062 (2 specimens); Point Leo, Western Port, F50064 (4 specimens); Flinders, Western Port, coll. 30 Jan. 1967, NMVF50066 (4 specimens); Flinders, Western Port, coll. 13 Jan. 1968, NMVF50067 (2 specimens); Sunderland Bay, Phillip Island, coll. 9 Dec. 1977, NMVF50068 (40 specimens); Kitty Miller Bay, Phillip Island, NMVF50069 (8 specimens); East of Grey River, Otways Coast, coll. 14 Aug. 1983, NMVF50070 (3 specimens); Corner Inlet, Doughboy Island, coll. 24 Nov. 1983, NMVF50160 (6 specimens).

DESCRIPTION: Size range of material examined 52 setigers, 9 mm long, < I mm wide to 60 setigers, 26 mm long, 2 mm wide (entire specimens). Pharynx with conical paragnaths on all Areas, some specimens with a few short bars also present on Area IV, arranged as follows (counts based on 36 specimens including II from the type series): I=2-8, usually 5-6; II=8-22; III=20-34; IV=18-33 cones and 0-3 short bars; V=9-19; VI=3-12, usually 7-10 in 2 rows; VII-VIII=66-115 large and small cones.

Notosetae all homogomph spinigers. Neurosetae heterogomph falcigers and homogomph spinigers in the dorsal fascicle and heterogomph falcigers and heterogomph spinigers in the ventral fascicle.

REMARKS: The description given here differs' slightly from the original description of Hutchings and Turvey (1982). They reported paragnath counts of V = 3-7 and VI = 11-24 whereas the material examined in this study is in the range V = 9-19 and VI = 3-12 (usually 7-10). The material examined here represents a wider size range than was available to Hutchings and Turvey. However, the differences also result in part from differing interpretations of the borders of Area VI: in the present study, counts for Area VI include only those paragnaths which make up the double row which is characteristic of *N*. biseriata.

Hutchings and Turvey reported homogomph spinigers in the ventral neuropodial fascicle in *N. biseriata*. The material examined in this study and Hutchings' and Turvey's working notes (Hutchings pers. comm.) confirm that the only setal types present in the ventral neuropodial fascicle are heterogomph spinigers and heterogomph falcigers.

Except as noted above the material examined here conforms to the description of Hutchings and Turvey (1982). The range of *N. biseriata* is here extended to include Western Australia, Victoria and Tasmania.

DISTRIBUTION: Western Australia, South Australia, Victoria and Tasmania. Known only from southern Australia.

HABITAT: Intertidal in algae and in rocks and sand.

Neanthes cricognatha Ehlers 1904

1904 Neanthes cricognatha Ehlers, p. 29, pl. 4, figs 3-7.

- 1982 Neanthes cricognatha Ehlers; Hutchings & Turvey, p. 110.
- 1971 Neanthes caudata delle Chiaje; Knox & Cameron, p. 28.
- 1975 Neanthes sp. 2 (sp. no. 604) Poore et al. p. 50.

MATERIAL EXAMINED: W.A.-Fremantle, NMVF50172. Bass Strait-Stn BSS 51 GSM, NMVF50166 (5

	N. cf. bassi sp. nov. $(n=4)$	N. bassi sp. nov. $(n = 19)$
Size range of material examined	14 setigers, 3 mm length, less than 1 mm width (anterior fragment) to 43 setigers, 9 mm length, 1.5 mm width (entire specimen)	14 setigers, 3 mm length, less than 1 mm width (anterior fragment) to 106 setigers, 51 mm length, 3 mm width (entire specimen)
Paragnaths on 1	2-4	Usually 0-1 (3 on one specimen 3 mm wide)
Paragnaths on 1V	2 specimens only have faint bars on one side	3-5 bars always present on both sides
Paragnaths on VII-VIII	5-8	10-20
Notopodia	Presetal lobe present in all specimens exceeding 1.5 mm width	Presetal lobe absent in specimens of all sizes
Neuropodia	Digitiform postsetal process present setigers 1-18 (1-11 on specimens less than 1 mm width)	Digitiform postsetal process present setigers 1-10 (absent on specimens less than 1 mm width)
Heterogomph falcigers appear in neuropodia	Setiger 2-3	Setiger 5-6 (rarely 2)
Pairs of dark patches on anterior dorsum	Absent	Usually present
Habitat	Mud sediment, 130-140 m	Variety of sediments, 18-51 m

 TABLE 2

 COMPARISON OF Neanthes bassi sp. nov. AND Neanthes cf. bassi sp. nov.

specimens); Stn BSS 83 DP, NMVF50167; Stn BSS 138 trawl, NMVF50168 (2 specimens); Stn BSS 155 SEB, NMVF50169 (3 specimens); Stn BSS 194 SEB, NMVF50170; Stn BSS 201 SEB, NMVF50171 (5 specimens). Additional material, NMV unregistered: Stns BSS 58, 59, 77, 81, 107, 108, 111, 112, 117, 127, 128, 134, 137, 153, 155, 158, 162, 170, 173, 178, 188, 197, 200, 203, 205, 207, 209 (total of 51 specimens).

Victoria – Werribee, Port Phillip Bay, coll. Aug. 1977, NMVF50079; Port Phillip Bay (Area 59 Stn 36, Knox and Cameron, 1971), NMVG1631; Port Phillip Bay, PPBES Stns: 907, 945, 974, NMV 3 unregistered specimens; West of Eagles Nest, coll. 19 Feb. 1966, NMVF50082; Shoreham, Western Port, coll. 20 Dec. 1965, NMVF50080; Flinders, Western Port coll. 31.1.1967, NMVF50081 (14 specimens); Western Port CPBS: Stn 21N, NMVF50164-5; Stn 32N, NMVF50161-2 (3 specimens); Stn 51N, NMVF50163; Corner Inlet, 4 km SE Barry Beach, coll. 24 Nov. 1983, NMVF50173 (2 specimens); Corner Inlet, 0.5 km S Granite Island, coll. 23 Nov. 1983, NMVF50174. Additional material, NMV unregistered, Western Port CPBS Stns 31S, 31N, 32S, 32N (total of 20 specimens).

N.S.W.-SBS: North Head, Sydney, 29 m, AMW198371 (2 specimens); Stn A2 sample 4, AMW198375; Stn B3 sample AMW198372; Stn C1 sample 5, AMW198374 (10 specimens); Stn D1 sample 2, AMW198373.

DESCRIPTION: Size range of material examined 25 setigers, 7 mm long, <1 mm wide to 32 setigers, 34 mm long, 4 mm wide (anterior fragments). Pharynx with conical paragnaths on all Areas arranged as follows (counts based on 23 specimens from Victoria and Bass Strait): 1=9-16; 11=22-45; 111=23-45; 1V=29-54; V-VIII a continuous band 3-5 deep dorsally, 5-8 deep ventrally. The largest paragnaths on the maxillary ring are found on Area 11 ('canine-like' curved teeth) and on the oral ring the largest paragnaths are those in the dorsal and dorsolateral positions (Areas V and VI).

Notopodia with three triangular lobes, neuropodia with two lobes and postsetal triangular process decreasing posteriorly. Notosetae homogomph spinigers, neurosetae homogomph spinigers and heterogomph falcigers throughout in dorsal and ventral fascicles. Heterogomph falcigers with long, almost rectangular blades and hooked distal tooth (figured by Ehlers 1904, pl. 4, fig. 5).

REMARKS: Neanthes cricognatha Ehlers 1904 has been synonymised with N. caudata (delle Chiaje 1828) and with N. arenaceodentata (Moore 1903) by Pettibone (1963), Day (1967), Imajima (1972) and Hartmann-Schröder (1982). 1 follow Hartman (1954) and Hutchings and Turvey (1982) in using the name N. cricognatha for Australian specimens. The Australian material examined in this study differs from material identified as Nereis (Neanthes) caudata from South Africa (Day 1967, p. 322, fig. 14.9i) in that the dorsal cirri of posterior setigers are located closer to the base of the notopodium than Day figured. The present material also differs from material encompassing a similar size range identified as *N. caudata* from Japan (Imajima 1972) in that Area 1 has fewer paragnaths (9-16) than that reported by Imajima (1 = 16-18).

DISTRIBUTION: Western Australia, South Australia, Tasmania, Victoria, New South Wales. Also recorded from New Zealand.

HABITAT: Intertidal to 140 m deep, more common subtidally, mostly from soft bottoms.

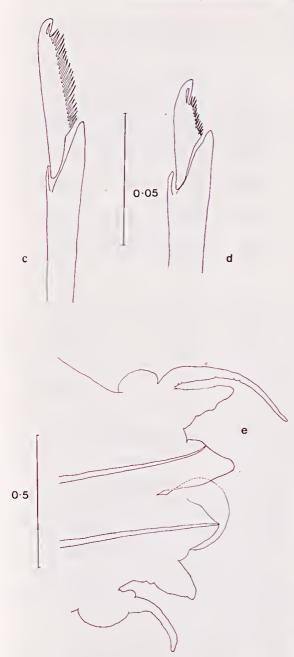
Neanthes flindersi sp. nov.

Fig. 2

MATERIAL: Holotype, NMVF50022 Bass Strait, S of Cape Otway (39°06.0'S 143°35.8'E) 95 m, fine sand, epibenthic sled, M. Gomon et al. on RV Hai Kung, 31 Jan. 1981 (Stn BSS 118). Paratypes, type locality, NMVF50023-8, AMW198697-9, BMNHZB1984.49-51, USNM097291-3. Bass Strait E of King Island (39°43.7'S 144°46.7'E), 53 m, fine sand (Stn BSS 129 trawl), NMVF50029 (early epitoke). Additional material, Bass Strait-Stn BSS 56 DN, NMVF50175 (3 specimens); Stn BSS 112 SEB, NMVF50176; Stn BSS 119 SEB, NMVF50177 (6 specimens); Stn BSS 128 trawl, NMVF50178-9; Stn BSS 171 SEB, NMVF50180 (2 specimens); Stn BSS 171 TAM, NMVF50181 (14 specimens); widespread western Bass Strait Stns BSS 55, 57, 75, 77, 82, 107, 112, 113, 116, 118, 120, 127, 129, 155, 182, 183, 193, 196, 198, 199, 200, 201, 203, 204, 205 (NMV unregistered, total of about 170 specimens). Tasman Sea-Taupo Seamount (Guyot), 33°14'S, 156°08'5"E, 137 m, AMW198700 (7 specimens).

DESCRIPTION: Holotype an anterior fragment of 48 setigers, 22 mm length, 3 mm maximum body width. Colour in alcohol pale yellow brown with no obvious markings or pigmentation. Prostomial width slightly exceeds length. Two pairs of dark red eyes shallowly embedded, anterior pair slightly larger and slightly further apart. One pair of dorsoventrally compressed palps with palpostyles. One pair of antennae about half length of prostomium. Four pairs of tentacular cirri, faintly annulated, longest extending to setiger 4. Jaws stout, dark brown, with 6 teeth. Pharynx with pale brown conical paragnaths on both rings, arranged as follows: 1=0; II=9, 6 in 2 crescent shaped rows; III=1; IV=15, 12; V=0; VI=2, 2 in a transverse row; VII-VIII=26 large and small cones in 2 rows.

Notopodia with two approximately equal lobes, smaller presetal lobe also present on setigers 8-20. Dorsal cirrus about 1.5 times length of dorsal notopodial lobe, becoming 2-2.5 times on posterior setigers. Notopodia thicker on anterior setigers, becoming elongate posteriorly. Neuropodia with two lobes, approximately equal on anterior setigers, ventral lobe becoming reduced posteriorly. Digitiform postsetal process present in neuropodia of anterior 12 setigers. Ventral cirrus basally attached, approximately half length of neuropodium on anterior setigers, becoming almost equal in length to neuropodium on posterior setigers (Fig. 2a,b). Notosetae all homogomph spinigers after setiger 2 (setigers 1 and 2 uniramous). Neurosetae



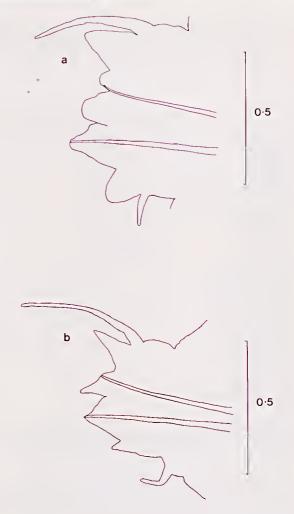


Fig. 2-*Neanthes flindersi* sp. nov. a, anterior view of 10th parapodium (holotype NMVF50022). b, anterior view of 47th parapodium (holotype NMVF50022). c, ventral neuropodial heterogomph falciger from setiger 10 (holotype NMVF50022). d, ventral neuropodial heterogomph falciger from setiger 47 (holotype NMVF50022). e, anterior view of 30th parapodium from early epitoke (paratype NMVF50029). Scalcs in mm.

heterogomph falcigers and homogomph spinigers in dorsal fascicle from setiger 1, ventral fascicle with homogomph spinigers and heterogomph falcigers (Fig. 2c, d) throughout. Heterogomph spinigers also present in ventral neuropodial fascicle of 6 anterior setigers but are absent posteriorly.

VARIATION: Variation not described for the holotype based on I4 paratypes (anterior fragments, size range 23 setigers, 5 mm length, 1 mm width, to 42 setigers, 21 mm length, 2.5 mm width; one entire specimen, NMVF50026, 58 setigers, 16 mm length, 1.5 mm width) and on 23 additional specimens from material listed above (entire specimens, size range 23 setigers, 6 mm length, I mm width, to 50 setigers, 23 mm length, 3 mm width). No obvious markings or pigmentation. Tentacular cirri faintly annulated, longest extending to setiger 2-7, usually 4-5. Pharynx with pale brown conical paragnaths on both rings, arranged as follows: I=0; II=4-12; II1=0-2 (usually 1); IV=6-21; V=0; VI=1-3 in a short transverse row; VII-VIII=16-30 in 2 rows of large and small cones.

Specimens >2 mm width with presetal notopodial

TABLE 3

	0								
	Area I	Area 111	Area V	Area VI	Area VII-VIII	Presetal (3rd) notopodial lobe (anterior	Postsetal (3rd) neuropodial lobe setigers)	Source of data	
N. agulhana Day 1963a	0	5-6	0	2-4	3-5 (1 R)	present	absent	Day 1963a	
N. biseriata Hutchings & Turvey 1982	2-8	20-34	9-19	5-12 (2 R)	66-115 (2-3 R)	present	present	Hutchings & Turvey 1982; this study	
N. dawydovi (Fauvel 1937)	0	4-7 °	0	2-3 (1 R)	3-5 (1 R)	absent	absent	Fauvel 1937	
N. flindersi sp. nov.	0	0-2	0	1-3	16-30 (2 R)	present	present	this study	
N. heteroculata (Hartmann-Schröder 1981)	0	7-12	0	2	17 (2 R)	absent	present	Hartmann-Schröder 1981	
N. kerguelensis (McIntosh 1885)	0-1	0-14	0	0-1*	0-7† (1 R)	present	present	this study	
<i>N. maculata</i> Wu Baoling & Sun Ruiping 1981	1	6-8	1	3-4 (1 R)	7 (1 R)	absent	absent	Wu Baoling & Sun Ruiping 1981	
<i>N. uniseriata</i> Hutchings & Turvey 1982	2-6	4-24	4-9	3-6 (1 R)	30-59 (2-3 R)	present	present	Hutchings & Turvey 1982; this study	

Neanthes Group 11B 1 (part; after Fauchald 1972). Comparison of species lacking fused falcigers, with fewer than 20 paragnaths on Area 111, with paragnaths in transverse row(s) on Area V1 and a band of 1-3 rows on Areas VII-VIII.

Explanation of abbreviations: R = suffix for number of transverse rows of paragnaths; * rarely 2-3 unilaterally; † rarely up to 12 on large specimens (see text).

lobe on about setigers 9-19 and also with neuropodial digitiform postsetal process on anterior 15-25 setigers. Heterogomph spinigers are present in the ventral fascicle of neurosetae anteriorly but are lost after setigers 3-14.

Anal cirri extend back 6-9 setigers.

Immature epitoke a gravid female (entire specimen, 72 setigers, 55 mm length, 3.5 mm width, NMVF50029) with paragnaths and setae as for atokous specimens. Eyes large, dark red. Dorsal and ventral cirri inflated basally on setigers 1-7. Epitokous parapodial modifications from setiger 17. Tubercles appearing at base of dorsal and ventral cirri, neuropodial postsetal digitiform process becoming lamellar (Fig. 2e).

REMARKS: Neanthes flindersi belongs to Fauchald's (1972) Group IIB I. Within this group only 7 species have been described which, like N. flindersi, have fewer than 20 paragnaths on Arca III, a transverse series on VI and a band of 2 rows on VII-VIII. Of the species listed in Table 3, N. agulhana Day 1963a most closely resembles N. flindersi but it may be distinguished by a pigmented band and spots on the anterior dorsum and by dorsal cirri becoming shorter on posterior setigers; N. flindersi is not pigmented and has dorsal cirri becoming longer posteriorly.

Among the species of *Neanthes* known from southern Australia, *N. flindersi* is most similar to *N*.

kerguelensis (McIntosh 1885) but can be distinguished from this and all known local species using the key. *N. flindersi* and *N. kerguelensis* also appear to differ in the distribution of heterogomph spinigers in the ventral neuropodial fascicle (see discussion of *N. kerguelensis*) but the variability of this potential taxonomic character is not yet fully understood.

ETYMOLOGY: *Neanthes flindersi* is named after Matthew Flinders who explored and charted much of the Australian coast.

DISTRIBUTION: Widespread western Bass Strait, one record eastern Bass Strait, one record from a seamount in the Tasman Sea. Known only from southeastern Australia.

HABITAT: Mostly carbonate sediments, 20-137 m.

Neanthes kerguelensis (McIntosh 1885) Fig. 3

- 1885 Nereis kerguelensis McIntosh, p. 225, pl. 35, figs 10-12, pl. 16a, figs 17, 18.
- 1897 Nereis kerguelensis McIntosh; Ehlers, p. 65, figs 81-93.

1901a Nereis kerguelensis McIntosh; Ehlers, p. 260.

1901b Nereis kerguelensis McIntosh; Ehlers, p. 105.

1906 Nereis kerguelensis McIntosh; Gravier, p. 29.

- 1907 Nereis kerguelensis McIntosh; Ehlers, p. 11.
- 1911 Nereis kerguelensis McIntosh; Gravier, p. 76.
- 1913 Nereis kerguelensis var. oligodonta Augener, p. 164.
- 1916 Nereis kerguelensis McIntosh; Benham, p. 122.
- 1916 Nereis kerguelensis McIntosh; Fauvel, p. 433.
- 1917 Nereis kerguelensis McIntosh; Fauvel, p. 203.
- 1924 Nereis kerguelensis McIntosh; Augener, p. 330.
- 1927a Nereis kerguelensis McIntosh; Augener, p. 134.
- 1927b Nereis kerguelensis McIntosh; Augener, p. 346.
- 1954 Neanthes kerguelensis (McIntosh); Hartman, p. 30.
- 1967 Neanthes kerguelensis (McIntosh); Hartman, p. 64.
- 1971 *Platynereis australis* (Schmarda); Knox & Cameron, p. 28 (partim.).
- 1980 Neanthes sp. Dorsey and Synnot, p. 158.
- 1982 Neanthes kerguelensis (McIntosh); Hutchings & Turvey, p. 113.

MATERIAL EXAMINED: W.A. – Point Peron, Rottnest Island, AMW18566; 3 mile reef, off Perth, 10.5 m, AMW18492; Fremantle, WAM94-84 (3 specimens).

S.A.-Penneshaw Jetty, Kangaroo Island, AMW18584; Rapid Bay, AMW18376 (5 specimens).

Tasmania – 16 km N of Circular Head, AME6310 (2 specimens) (examined by Benham 1916); Pegleg Cove, Deal 1sland, 10-12 m, NMVF50028; Cape Sorell, AMW3661 (3 specimens); Pilot Bay, Cape Sorell, NMVF50047 (2 specimens).

Macquarie Island – Macquarie Island, AMW753.

Bass Strait – Stn BSS 77 GSM, NMVF50182, Stn BSS 117 SEB, NMVF50183 (2 specimens); Stn BSS 156 SEB, NMVF50184; Stn BSS 191 DR, NMVF50185; Stn BSS 201 SEB, NMVF50186 (15 specimens). Additional material, NMV unregistered: Stns BSS 72, 73, 77, 107-109, 112-113, 116, 117, 119, 127, 128, 131-133, 137-139, 152, 154, 156-158, 163, 171, 173, 182, 187, 188, 190, 191, 194, 197-201, 203-205, 209, 212 (total of approximately 130 specimens).

Victoria-Grey Point, Lorne, NMVF50031 (2 specimens); Aireys Inlet, NMVF50046; Black Rock, Connewarre, NMVF50134-5 (3 specimens) (*Neanthes* sp. of Dorsey & Synnot 1980); Port Phillip Survey Area 59 Stn 24, NMVG1640 (*Platymereis australis* of Knox & Cameron 1971); Port Phillip Bay, Sandringham Breakwater, NMVF50045; Merricks, Western Port, NMVF50030; Cape Woolamai, 30 m deep, NMVF50044 (2 specimens); Kilcunda, NMVF50043; W of Eagles Nest, NMVF50041 (2 specimens); near Eagles Nest, NMVF50042; Corner Inlet, 2 km S Sunday Island, 9 m; coll. 22 Nov. 1983, male epitoke, NMVF50187.

DESCRIPTION: Size range 35 setigers, 5 mm length, less than 1 mm width (entire specimen) to 32 setigers, 34 mm length, 5 mm width (anterior fragment). Tentacular cirri extending 4-8 setigers. Pharynx with conical to domed paragnaths sometimes faint or fused into an irregular mass. Paragnaths arranged as follows: I=0, rarely 1; II=3-18; III=0-14, usually 0-4; IV=4-26; V=0; VI=0-1 (2-3 on one side only in 3 specimens from

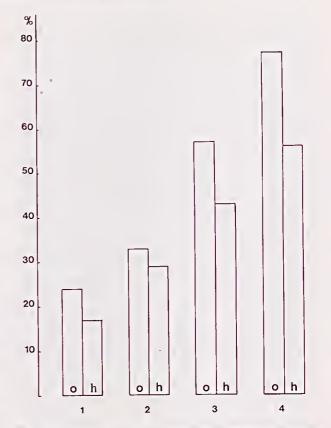


Fig. 3-Neanthes kerguelensis (McIntosh 1885). Frequency histogram showing percentage presence of oral ring paragnaths (o) and heterogomph spinigers (h) in 4 size classes. $1 \le 1.5$ mm wide, n=41, 2=2, 2.5 mm wide, n=21; 3=3, 3.5 mm wide, n=14; 4=4-6 mm wide, n=9. Widths excluding parapodia, measured to nearest 0.5 mm.

Kangaroo Island, S.A., AMW18377); V11-V11I = 0-7 (12 on one very large specimen, 6 mm wide, NMVF50030).

Notopodia with two lobes throughout, specimens wider than 1 mm with presetal notopodial lobe on at least setigers 9-14 (up to setigers 4-28 on specimens>4 mm width). Dorsal cirrus approximately 1 to 1.5 times length of dorsal notopodial lobe, becoming 1.5 to 2 times length on posterior setigers. Neuropodia with two lobes throughout, specimens wider than about 1 mm with digitiform postsetal process on anterior 20-30 setigers, reducing in size posteriorly. Ventral neuropodial lobe slightly reduced posteriorly, ventral cirrus basally attached, approximately 3/4 length of neuropodium throughout. Notosetae homogomph spinigers. Dorsal fascicle of neurosetae heterogomph falcigers and homogomph spinigers from setiger 1, ventral fascicle with homogomph spinigers and heterogomph falcigers throughout. Heterogomph spinigers may also be present in the ventral neuropodium in a variable number of anterior setigers but are absent at setiger 8 and all posterior setigers.

The only male epitoke available (NMVF50187) had modified parapodia commencing at setiger 15 but agrees

in all other respects with the description of male and female epitokcs given by Ehlers (1897, p. 65, pl. 4, fig. 81-93).

REMARKS: The Southern Hemisphere synonymies included here indicate considerable variability in the number of oral ring paragnaths. The original description (McIntosh 1885) gives an oral ring paragnath formula of V = 0, V1 = 1 on each side, V11 = V111 = 5-6. Augener (1913) described var. oligodonta from Western Australia with V1 = 1, V11 - V111 = 3 on the oral ring. He later examined material from New Zealand and southeastern Australia (Augener 1924b, 1927a) which also had few or no oral ring paragnaths and noted that specimens from warmer seas tended to a reduction in numbers of paragnaths on 1, 111 and the oral ring compared with Antarctic and sub-Antarctic material. Hartman (1954) recorded an oral ring formula of V=0, V1=1, V11-V111=9 for South Australian material and Hutchings and Turvey (1982) recorded V=0, occasionally 1, V1 = 0, V11 - V111 = 0 - 4 and noted that some individuals were lacking or had very pale oral ring paragnaths.

In this study a detailed examination was made of variation in setae and paragnaths in 85 specimens from a variety of habitats in the Bass Strait region. The size of animals examined ranged from less than 1 mm to 6 mm wide although about half the sample was less than about 1.5 mm wide. Figure 3 presents percentage frequency of occurrence of oral ring paragnaths and heterogomph spinigers as a function of size class and shows that the presence of these two characters is related to the size of the worm. Some of the observed variation is however not explained by size and appears to be unrelated to other morphological characters or to habitat.

The variability observed within *N. kerguelensis* in this study from a restricted area exceeds the variability observed by earlier workers in the Southern Hemisphere and suggests problems in distinguishing material from more distant localities. Hartmann-Schröder (1981) gave a partial Northern Hemisphere synonymy, a distribution from Antarctica to north and central Atlantic and Mediterranean and habitat range from intertidal to 5 000 m. Further work is required to examine variation within and between populations from these widely separated localities and habitats.

The variability observed in *N. kerguelensis* may also present problems in distinguishing that species from *N. flindersi.* Juvenile specimens (<1 mm width) will be indeterminable unless absence of heterogomph spinigers from the anterior 6-10 setigers can be determined with certainty. Heterogomph spinigers are always present anteriorly in *N. flindersi* but are absent in some specimens of *N. kerguelensis.* Specific determinations based on oral ring paragnath counts should be possible in all material exceeding 1 mm in width.

DISTRIBUTION: Southwestern Western Australia, South Australia, Tasmania, Victoria, New South Wales. Widely recorded in Northern and Southern Hemispheres.

HABITAT: Associated with fouling communities, inter-

tidal in rocks and sand on sheltered and exposed coasts, soft bottom benthos to 115 m deep.

Neanthes succinea (Leuckart 1847) Fig. 4

- 1847 Nereis succinea Leuckart, p. 154, pl. 2, figs 9, 11.
- 1934 Nereis oxypoda (Marenzeller); Monro, p. 362. (partim.)
- 1938 Nereis oxypoda (Marenzeller); Monro, p. 614, figs 1-5.
- 1963 Nereis (Neanthes) succinea Leuckart; Pettibone, p. 165, figs 44a-e, 45a-d.
- 1967. Nereis (Neanthes) succinea Leuckart; Day, p. 321, fig. 14.9a-e.
- 1972 Neanthes succinea (Leuckart); Imajima, p. 108, figs 32a-k, 37.
- 1984 Neanthes oxypoda (Marenzeller); Hutchings & Murray, p. 37.

MATERIAL EXAMINED: W.A. – Crawley Bay, Swan River, immature fcmale epitoke, gravid, coll. summer 1930, BMNHZK 1938.10.31.7; Swan River, immature female epitoke, gravid, coll. 17 Aug. 1935, BMNHZK 1938.10.31.8; Pelican Point, Swan River, 3 specimens, including 1 immature female epitoke, gravid, coll. 12 April 1930, BMNHZK 1938.10.31.9-10 (material identified as *Nereis oxypoda* by Monro 1938).

Victoria-Hobsons Bay, PPBES: Stn 128, NMVF50084, F50085 (6 specimens); Stn 130, NMVF50086, F50087; Stn 132, NMVF50088; Stn 136, 3, NMVF50089; Stn 134, NMVF50090 (immature epitoke), Hobsons Bay, Yarra River at Westgate Bridge, coll. 10 April, 1984, 9 m, NMVF50128; Yarra River, Newport Powerhouse site, many, male and female epitokes, NMVG1109; Port Phillip Bay off Yarra River mouth coll. 20 Oct. 1978, 1, sub-epitoke, NMVF50083; Maribrynong River, at Sims Street, coll. 4 Mar. 1981, 1, sub-epitoke, NMVF50129.

N.S.W. – Port Hacking: Stn 630, AMW195244 (2 specimens); Stn 631, AMW195222; Stn 641, AMW195305 (2 specimens). Hawkesbury River: Stn D2-2, AMW196461; Stn D2-3, AMW196462 (2 specimens); Stn D4-3, AMW196463. Lake Macquarie, Zostera beds, AMW17830. (Full locality data given by Hutchings & Mutray 1984).

China-Amoy, coll. T. Y. Chen, immature female epitoke, gravid, BMNHZK 1933.3.2.40 (1 of 3 specimens identified as *Nereis oxypoda* by Monro 1934, see below).

U.S.A.-Sippiwissett, Mass. coll. 25 Jan. 1953, M. H. Pettibone, USNM27799 (23 specimens).

Canada–Off Sheldrake Island, Miramichi River, Nova Scotia, coll. 28 July 1952, USNM35807 (9 epitokes).

Netherlands – E of Schokland, Zuiderzee, coll. 17 Aug. 1905, USNM27897 (3 specimens).

W. Germany-Ems River, freshwater, coll. 1954/55, HZMP13065, P13067, V13071 (30 specimens); Helgoland, HZMP16369 (2 specimens); Kugelbakc, Cuxhaven, HZMV10925 (2 specimens); Americahafen, Cuxhaven, HZMV9984, V10693 (4 specimens).

NEANTHES (POLYCHAETA:NEREIDIDAE) FROM VICTORIA

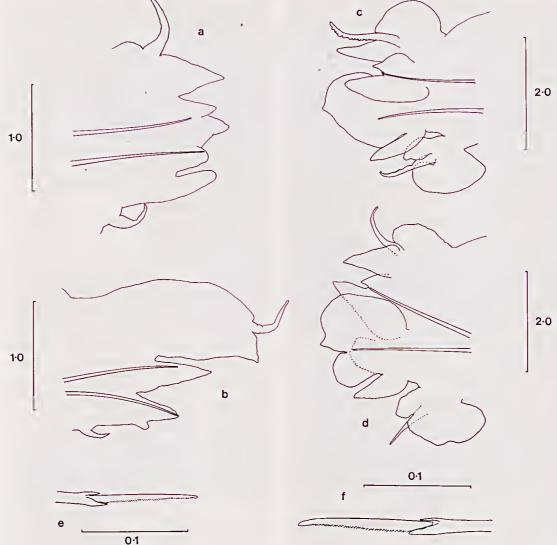


Fig. 4–*Neanthes succinea* (Leuckart 1847) a, posterior view of 10th parapodium (NMVF50087). b, anterior view of 39th parapodium (NMVF50087). c, anterior view of 35th parapodium from immature male epitoke (NMVG1109), part). d, posterior view of 30th parapodium from immature female epitoke NMVG1109, part). e, ventral neuropodial heterogomph falciger, setiger 10 (atoke, NMVF50087). f, ventral neuropodial heterogomph falciger, setiger 7 (immature male epitoke, NMVG1109, part). Scales in mm.

DESCRIPTION: Description based solely on 28 specimens selected from the Australian material listed above. Size range of material examined 30 setigers, 5 mm long, less than 1 mm wide (entire specimens) to 89 setigers, 155 mm long, 8 mm wide (anterior fragment). Prostomial length slightly exceeds width. Two pairs of red eyes. One pair of palps with small palpostyles, one pair of antennae about $\frac{1}{3}$ as long as prostomium. Four pairs of tentacular cirri, longest extending 3-6 setigers posteriorly. Jaws translucent brown with about 5-6 teeth. Pharynx with conical paragnaths on all Areas, arranged as follows: I = 0-5 (usually 2-3) in longitudinal H series; I1 = 7-23, 2 rows in a crescent; I11 = 2-42, usually 20-30 in an oval group; IV = 13-34 in 2-3 curved rows, tapering to 1 row close to the base of the maxillae; V = 0-4, usually 2-3 in a triangle; VI = 6-14 in a roughly circular group; VII-VIII = 36-62 in 2-3 rows.

Notopodia anteriorly with three triangular lobes and basally attached dorsal cirrus, all approximately equal in length. Dorsal lobe becoming expanded posteriorly, lamellar in form with dorsal cirrus attached subdistally (dorsal cirrus distally attached on posterior most segments). Median lobe becoming reduced posteriorly, may be absent from about setiger 25 on specimens <2 mm body width but persisting to setiger 40 to 50 at least on larger specimens. Neuropodia with two triangular lobes, approximatcly equal in length throughout and prominent postsetal lobe of approximately equal length, decreasing slightly on posteriormost setigers (Fig. 4a, b). Notosetae homogomph spinigers. Dorsal fascicle of neurosetae homogomph spinigers and heterogomph falcigers, ventral fascicle of neurosetae heterogomph falcigers are distinctively long and narrow with blunt rounded tips (Fig. 4e, f). Several immature epitokes with homogomph and heterogomph spinigers throughout, falcigers absent. Natatory setae present only in advanced epitokes (NMVG1109). Anal cirri extend back over 7-14 setigers.

Male epitokes with dorsal cirri inflated on setigers 1-7, ventral cirri inflated on setigers 1-5. Epitokous parapodia from setiger 15; ventral surface of dorsal cirri and dorsal surface of ventral cirri crenulate, inflated lobes at the bases of both cirri. Median notopodial lobe reduced posteriorly, dorsal and ventral notopodial lobes elongate, lamellar, median notopodial lobe reduced posteriorly. Dorsal neuropodial lobe inflated, discoid, ventral neuropodial lobe digitiform (Fig. 4c). Posterior most setigers approximately as for atokes: dorsal notopodial lobe an clongate triangle, remaining lobes shorter triangles.

Female epitokes with dorsal cirri inflated on setigers 1-5, ventral cirri inflated on setigers 1-3. Epitokous parapodia appear variably from setiger 16-20, usually 18-20. Dorsal and ventral cirri smooth throughout, a single dorsally inflated lobe at the base of the dorsal cirri, a pair of inflated lobes at the base of the ventral cirri. Median notopodial lobe reduced posteriorly, remaining notopodial lobes elongate triangles. Dorsal neuropodial lobe divided along the line of the neuroaciculum into unequal discoid lobes, the dorsal lobe being the larger. Ventral neuropodial lobe digitiform (Fig. 4d). Posteriormost setigers approximately as for atokes.

REMARKS: The type of N. succinea is in poor condition (G. Hartmann-Schröder, pers. comm.). However, material has been examined from a range of Northern Hemisphere localities including the type locality (Helgoland and Cuxhaven, German North Sea). The Australian material described here agrees with the Northern Hemisphere material in every detail except for the variability observed in the paragnath counts of Area 111: several Australian specimens, including 9 specimens from N.S.W. and 5 specimens from W.A. have only 2-4 paragnaths here, compared with 20-30 on most Victorian specimens and on all Northern Hemisphere specimens examined. This character state does not appear to be related to size of specimen or to any other morphological character and is considered here as part of the normal intraspecific variation of N. succinea (in this study N. bassi and N. kerguelensis were also found to exhibit considerable variability in paragnath counts on Area 111).

Two Australian records of *Neanthes* (*Nectonean-thes*) oxypoda (Marenzeller 1879) are included above in

the synonymy of N. succinea. This material (Monro 1938, Hutchings & Murray 1984) includes epitokes at various stages of development; these specimens differ from atokous N. succinea only in the expected epitokal modifications of parapodia and setae (as noted in the description above, these modifications include the loss of neuropodial falcigers in some immature epitokes). Paragnath counts and unmodified parapodia from the natatory region do not appear to vary significantly with the development of epitoky and several immature epitokes retain a few neuropodial falcigers, the form of which is distinctive (Fig. 4f). The epitokes examined here also agree with the detailed description given by Pettibone (1963) of epitokous modifications in N. succinea from N. America and all Australian records are thus referred to this species.

Monro (1934, p. 362) reported 3 specimens of N. oxypoda from Amoy, China, and noted that: 'The specimen collected by Chen corresponds exactly to Marenzeller's account. The other two show a marked variation in the arrangement of the paragnaths.' The specimen collected by Chen (BMNHZK 1933.3.2.40) agrees in every respect with the N. succinea epitokes examined in this study and is included in the above synonomy. The remaining 2 specimens (BMNHZK1926. 4.27.22-23) differ from N. succinea in that a continuous band of paragnaths 8-10 deep is present through Areas V-VIII of the oral ring. These specimens appear to agree in all other respects with the N. succinea epitokes examined in this study but in view of the substantial deviation from the paragnath counts of that species 1 prefer to retain this distinct form as Neanthes (Nectoneanthes) oxypoda var. A third specimen of N. oxypoda var. examined in this study, a gravid immature female epitoke (USNM22240), appears to have been split from Chen's collection before its examination by Monro; labels of both specimens carry the information 'Amoy, China, coll. T. Y. Chen, No. 27'. Imajima (1972) has also described and figured this form (as Nectoneanthes oxypoda) from 7 localities in southern Japan.

In summary, the above findings show that published records of *Neanthes* (*Nectoneanthes*) oxypoda from Australia, China and Japan confuse two distinct forms. One form, designated here as *N. oxypoda* var., is known only from epitokes from China and Japan and is probably an undescribed species. Atokous material will be required before this form can be given an accurate genetic placement. Monro (1934), and probably all remaining records including the original description of *N. oxypoda* (Marenzeller 1879), appcar to describe epitokes of *N. succinea*. If Marenzeller's type material can be located and agrees with his original description then *N. oxypoda* would become a junior synonym of *N. succinea*.

The genus Nectoneanthes Imajima 1972 was erected for species of Neanthes which lack neuropodial falcigers. Four species are currently placed in Nectoneanthes: N. alatopalpis (Wesenberg-Lund 1949), N. imajimai Imajima 1972, N. oxypoda (Marenzeller 1879, type species and N. multignatha Wu Boaling & Sun Ruiping 1981. Nectoneanthes differs from Neanthes only in the lack of neuropodial falcigers and the expansion of the superior notopodial lobe on median setigers, characters which are associated with the development of epitoky. Group 1 of Fauchald's (1972) subdivision of *Neanthes* was also created for species lacking falcigers and contains four species which were not included in *Nectoneanthes* by Imajima (1972). At least one species in Fauchald's Group I, *N. virens* (Sars 1835) does possess neuropodial falcigers although they may be lost in adult worms (Pettibone 1963). Both *Nectoneanthes* Imajima 1972 and *Neanthes* Group 1 (Fauchald 1972) appear to be based on inadequate material and require reappraisal. Neither group is represented in Australian material.

I cite Leuckart 1847 as author of *N. succinea*, not Frey & Leuckart 1847, as is widely cited elsewhere. This interpretation is due to Mr. A. Muir (pers. comm.) who drew my attention to the relevant passage of the introduction to Frey and Leuckart, 1847 which states (in translation from the German: '... the last paper on the fauna of Helgoland ... is exclusively a property of Dr Leuckart'.

DISTRIBUTION: Western Australia (Swan River), Victoria (Yarra and Maribyrnong Rivers), New South Wales (Port Hacking, Hawkesbury River, and Lake Macquarie). Widely recorded in Northern and Southern Hemispheres.

HABITAT: Appears to be restricted to estuaries (in Australia).

Neanthes uniseriata Hutchings & Turvey 1982

1982 Neanthes uniseriata Hutchings & Turvey, p. 113, fig. 8a-c, table 8.

MATERIAL EXAMINED: S.A. – Victor Harbour (18A), 14 paratypes, AMW18433; Cape de Couedic, Kangaroo Island, 50 paratypes, AMW18432. (full locality data given by Hutchings & Turvey 1982).

Vic. – Anglesea Reef, coll. 16 Oct. 1976, NMVF50078 (2 specimens); Somers, Western Port, NMVF50073; Shoreham Reef, Western Port, coll. Jan. 1967, NMVF50074; Merricks, Western Port, coll. 1969, NMVF50075; Cat Bay, Phillip Island, coll. 18 Feb. 1978, NMVF50076 (40 specimens); Sunderlands Bay, Phillip Island, coll. 3 July 1979, NMVF50077; Kilcunda, coll. Jan. 1966, NMVF50071, F50072 (10 specimens).

DESCRIPTION: Size range of material examined 41 setigers, 5 mm long, <1 mm wide to 76 setigers, 31 mm long, 3 mm wide (entire specimens). Pharynx with conical paragnaths on all Areas, some specimens with a few short bars also present on Area IV, arranged as follows (counts based on 30 specimens, including 9 from the type series): I=2-6, usually 4-5; II=3-13; III=4-24, usually 1I-22; IV=8-26 cones and 0-3 short bars; V=4-9, usually 5-7; VI=3-6 in a single arc occasionally including 1 or 2 behind; VII-VIII=30-59 large cones only.

Notosetae all homogomph spinigers. Neurosetae heterogomph falcigers and homogomph spinigers throughout in the dorsal fascicle and heterogomph falcigers and heterogomph spinigers in the ventral fascicle. REMARKS: The Victorian material agrees with the description given by Hutchings and Turvey (1982) and with the type series from South Australia. The present author disagrees with Hutchings and Turvey on the interpretation of the borders of Area VI of the pharynx and thus there are slight differences in paragnath formulae from those given by Hutchings and Turvey. As with *N. biseriata* counts for Area VI only include those paragnaths which form the single arc which characterises *N. uniseriata* even though part of the ventral band of paragnaths and some paragnaths on Area VI may be interpreted as extending into Area VI.

DISTRIBUTION: South Australia and Victoria. Known only from southeastern Australia.

HABITAT: Intertidal in algae and in rocks and sand.

Neanthes vaalii Kinberg 1866

1866 Neanthes vaalii Kinberg, p. 171.

- 1981 Neanthes vaalii Kinberg; Hartmann-Schröder, p. 42, figs 88-93.
- 1982 Neanthes vaalii Kinberg; Hutchings & Turvey, p. 116.
- 1984 Neanthes vaalii Kinberg; Hutchings & Murray, p. 40.

MATERIAL EXAMINED: W.A. – King River, Albany, coll. 6 Mar. 1971, WAM49-74 (part); Walpole Inlet, Walpole, coll. 5-10 Aug. 1973, WAM97-84 (many specimens).

S.A. – Waldegrave Island, coll. 25 Oct. 1973, AMW18490; Thevenard (nr. Ceduna), coll. 4 Feb. 1970, AMW4341 (3 specimens).

Tasmania – Derwent River, coll. 4 May 1982, NMVF50039 (2 specimens); Huon River Site 12, coll. Feb. 1976, AMW11076; Huon River Site 14, coll. 5 Feb. 1976, AMW11096 (2 specimens).

Victoria-Port Phillip Bay, Ricketts Point, coll. Feb. 1964, NMVF50038 (5 specimens); Western Port CPBS: Stn 000, NMVF50227 (34 specimens); Stn 02N, NMVF50228 (2 specimens); Stn 03N, NMVF50229 (13 specimens); Point Leo, coll. 18 Jan. 1969, NMVF50036; Hastings, coll. 1 Mar. 1962, NMVF50037 (epitoke); Corinella, coll. 8 Feb. 1969, NMVF50035 (3 specimens); Western Port Canons Creek, coll. 1 April 1970, NMVF50034; Corner Inlet, 3.5 km WSW of McLoughlans Beach, 2 m, 22 Nov. 1983, NMVF50188; S of Manns Beach, intertidal, 19 Nov. 1983, NMVF50189-90 (11 specimens); 1 km SE of Manns Beach, 0.5 m, 22 Nov. 1983, NMVF50191; 0.5 km W of Port Welshpool, intertidal, 20 Nov. 1983, NMVF50192; cove on N side Doughboy Island, 2 m, 24 Nov. 1983, NMVF50193; N end of Long Island, 0.1 m, 23 Nov. 1983, NMVF50194 (2 specimens); Gippsland Lakes GRES Stn 3073, NMVF50033 (2 specimens).

N.S.W. – Batemans Bay, coll. 10 Jan. 1970, NMVF50032.

DESCRIPTION: Size range 29 setigers, 5 mm length, <1 mm width (anterior fragment) to 89 setigers, 31 mm length, 3 mm width (entire specimen). Large specimens with even dark blue/brown pigmentation on anterior dorsum, smaller specimens pale. Tentacular cirri long,

longest extending 9-10 setigers. Pharynx with conical paragnaths on both rings and smooth bars also present on IV only. Paragnaths arranged as follows: I = 1-4 (usually 2 or 3) in longitudinal series; II = 7-17; III = 19-28 often with 1 or 2 separate at each side; IV = 16-33 cones and I-4 smooth bars; V = 3 in a triangle, rarely only 1 or 2; VI = 3-5 in a compact group, rarely with fewer (0-2) on one side; VII-VIII = 37-59 in 2-3 rows extending on to VI.

Notopodia with two lobes approximately equal in size throughout, large specimens also with presetal notopodial lobe on about setigers 6-20 (presetal lobe present on fewer setigers on smaller specimens and absent on specimens less than about 1.5 mm wide). Dorsal cirrus approximately twice length of notopodial lobes. Neuropodia with two lobes, ventral lobe slightly smaller. Digitiform postsetal process absent. Ventral cirrus extending to tip of ventral neuropodial lobe. No marked change in relative proportions of parapodial lobes on posterior segments. Notosetae homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers in dorsal fascicle in all setigers, heterogomph spinigers and heterogomph falcigers in ventral fascicle in all setigers.

Anal cirri extend back 4-8 setigers.

Male epitoke (NMVF50037) 102 setigers, fully mature. Eyes large, lacking pigment (in alcohol). Paragnaths as for atokous specimens. Dorsal cirri of anterior 7 setigers and ventral cirri of anterior 5 setigers basally inflated. Setigers 4-17 with presetal notopodial lobe. Parapodia showing epitokal modifications from setiger 18: ventral surface of dorsal cirri crenulate, expanded lamellar lobes dorsally at the base of the dorsal cirrus and ventrally at the base of the ventral cirrus, digitiform lobes situated medially at the base of each cirrus, large lamellar postsetal lobe in neuropodia. Specialised natatory setae present in all modified parapodia. Pygidium with an expanded rosette of many digitiform papillae. Anal cirri appear to be absent. Epitokous modifications agree with the descriptions given by Hartman (1954, p. 28, fig. 24). Hartmann-Schröder (1981, p. 42, figs 91, 92) described modifications of an immature epitoke.

REMARKS: The presence of smooth bar paragnaths in addition to cones on Area IV has not been reported for *N. vaalii* but was noted on all material examined in this study.

DISTRIBUTION: Temperate Australia from Geraldton, Western Australia to Careel Bay, New South Wales. Known only from Australia and New Zealand.

HABITAT: Sheltered coasts, associated with fouling communities, oysters, mussel clumps, under rocks, in *Zostera*; intertidal to 4 m deep.

Neanthes cricognatha and N. kerguelensis are cosmopolitan species or species complexes; both occur in a variety of habitats but in Australia they occur most commonly on the continental shelf of Bass Strait. Two new species described in this study also occur in Bass Strait; N. bassi, which is also recorded from Port Phillip Bay, and N. flindersi, which appears to be restricted to the continental shelf. The *Neanthes* fauna of Bass Strait is thus qualitatively and quantitatively different from that of Port Phillip Bay and Western Port (Table 4).

Neanthes succinea is recorded here from Australia for the first time. This species is known from a variety of marine and estuarine habitats elsewhere in its range (Pettibone 1963) but in Australia it appears to be restricted to a few estuaries. Most of these localities are associated with international ports and it has been suggested that these records may represent accidental introductions (K. Fauchald pers. comm.).

Neanthes biseriata and N. uniseriata are closely related species which are usually collected from exposed rocky shores. Both species also occur at less exposed sites but are rarely collected with N. vaalii, which is widespread at sheltered localities and in seagrass.

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NEANTHES (POLYCHAETA:NEREIDIDAE) FROM VICTORIA

	Bass Strait benthos (BSS)	Port Phillip Bay benthos (PPBES)	Western Port benthos (CPBS)	Exposed rocky shores	Sheltercd coast rock & seagrass
N. bassi	uncommon	uncommon	b		_
N. biseriata		-	-	common	uncommon
N. cricognatha	common	uncommon	common	uncommon	uncommon
N. flindersi	common	-	_	-	-
N. kerguelensis	common		-	uncommon	uncommon
N. succinea		common*	-	_	-
N, uniseriata	-		-	common	uncommon
N. vaalii	-	-	uncommon	-	common

	TABLE	: 4		
SUMMARY OF ECOLOGICAL	DATA FOR	VICTORIAN	SPECIES OF	Neanthes

Species are defined as common in benthic surveys if they occur at 10% or more of stations. Common for exposed and sheltered sites is based on qualitative records presented in this study.

* Yarra and Maribyrnong Rivers only.

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APPENDIX

Species of *Neanthes* Kinberg 1866, with reference to original descriptions, type locality and grouping according to Fauchald (1972) (after Hartman 1959, 1965).

- * denotes any reference that has not been seen in the original by me.
- † denotes any Fauchald grouping that has been emended or is made for the first time on my authority.

The Fauchald grouping is repeated here:

- 1 Falcigers absent
- II Falcigers present (or presence or absence not known) A Parapodial lobes with papillae
 - B Parapodial lobes smooth
 - 1 Dorsal lobe of notopodia barely longer than the other parapodial lobes, usually triangular
 - 2 Dorsal lobe of notopodia longer than the other lobes a Dorsal lobes large thick or foliose
 - b Dorsal lobes slender, long in all setigers

c Dorsal lobes prolonged in posterior setigers C Development of parapodial lobes unknown

- N. abyssorum Hartman 1967: 63-4, pl. 16, fig. a, b. Bransfield Strait, Antarctica, ca. 2,500 m. Group IIB 1⁺.
- N. agnesiae (Augener 1918: 194-7, pl. 3, figs 69-71, pl. 4 figs 76-7), as Nereis (Alitta) agnesiae. Southwest Africa. Group 1.
- N. agulhana (Day 1963a: 406-7, textfig. 6d-j), as Nereis (Neanthes) agulhana. South Africa. Group IIB 1.
- N. angusticollis (Augener 1913: 145-9, pl. 2, fig. 14u, textfig. 13a-d), as Nereis angusticollis. Perth, Shark Bay, southwestern Australia. HOMONYM. Group 11B 1.
- N. arenaceodentata (Moore 1903: 720-3, pl. 40, figs 1-10), as Nereis arenaceodentata. Massachusetts. Group IIB 1⁺.
- N. articulata Knox, 1960: 121-2, figs 174-9. Chatham Is, New Zealand. Group IIB 2a.
- N. augeneri (Gravier & Dantan 1934: 52-4, figs 12-13), as Nereis (Neauthes) augeneri. Annam. Group 11C.
- N. bassi sp. nov., see above. Bass Strait, southern Australia. Group 11B 1⁺.
- N. belawanensis (Pflugfelder 1933: 72-3, fig. 13), as Nereis belawensis. Sumatra. Group IIB 1.
- N. biseriata Hutchings & Turvey 1982: 108-110, fig. 6a-d. South Australia. Group 11B 1⁺.
- N. brandti (Malmgren 1866: 183-4), as Alitta brandti. Siberia. Group 11B 2a. Sce also Hartman, 1968: 523.
- N. caudata (delle Chiaje 1828, in Quatrefages 1865: 551.)*, as Spio caudatus, Southern Europe. Group IIB 1. See also Fauvel, 1923: 347-8, fig. 135a-e.
- N. chilkaensis (Southern 1921: 584-9, pl. 22, fig. a-r, textfig. 4a-c), as Nereis (Nereis) chilkaensis. Chilka Lake, India. Group IIB 1. See also Fauvel, 1923: 94-5.
- N. chingrighattensis (Fauvel 1932: 90-1, fig. 14a-h), as Nereis chingrighattensis. Chingrighatta, India, Group 1.
- N. cortezi Kudenov 1979: 118-20, fig. 2a-h. Gulf of California. Group IIB 2c.
- N. cricognatha (Ehlers 1904: 29-30, pl. 4, fig. 3-7), as Nereis cricognatha. New Zealand. Group IIB 1⁺. See also this study.
- N. crucifera (Grube 1878: 80-1, pl. 5, fig. 6), as Nereis (Lycoris) crucifera. Philippine Islands, Group 11B 2b.
- N. dawydovi (Fauvel 1937: 297-9, fig. 1a-k), as Nereis dawydovi, Indo-China. Group 11B 1.
- N. donghaiensis Wu Boaling & Sun Ruiping 1981: 215-6 (English summary), fig. 82a-c. Fukien, China. Group 11B 1⁺.
- N. diversicolor (Müller 1776: 217), as Nereis diversicolor. Denmark. See *Hediste diversicolor*, fide Hartmann-Schröder 1971, Fauchald 1977a.
- N. flava Wu Boaling & Sun Ruiping 1981: 218 (English summary), fig. 89a-1. Hopei, China. Group 11B 1⁺.
- N, flindersi sp. nov. see above. Bass Strait, southern Australia. Group 11B 1[†].
- N. fucata (Savigny 1818: 210-1), as Lycoris fucata. Mediterranean Sea. Group 11B 2a.
- N. galetae Fauchald 1977b: 26-7, fig. 6a-c. Panama. Group IIB 1.
- N. glandicincta (Southern 1921: 589-93, pl. 23, fig 9a-1, textfig. 5a-c), as Nereis (Nereis) glandicincta. Calcutta, India. Group 11B 1. See also Fauvel 1932: 92-3.
- N. helenae Kinberg 1866: 172. St. Helena Island. Incompletely known; may include Neanthes nanciae.
- N. heteroculata Hartmann-Schröder 1981: 30-1, fig. 9-13. Bay of Biscay, 4 700 m. Group IIB 1.
- N. indica (Kinberg 1866: 169), as Nereis indica. Group 11B 1. See also Willey 1905: 270-1; Fauvel 1932: 96.

- N. indica brunnea Day 1957: 79-81, fig. 4h-n. Mozambique 1s, South Africa. Group IIB I.
- N. isolata Hutchings & Turvey 1982: 111-3, fig. 7a-d. South Australia. Group 11B 1⁺.
- N. japonica lzuka 1908: 294-305, textfig. Ia, c. Japan. Group 11B 2a. See also lzuka, 1912: 163-9, pl. 17, fig. 14-16, 18.
- N. kerguelensis (McIntosh 1885: 225-7, pl. 35, fig. 10-12), as Nereis kerguelensis. Kerguelen Islands. Group IIB 1. See also this study.
- N. latipalpa (Schmarda 1861: 104-5, pl. 31, fig. 244), as Nereis latipalpa. Capc of Good Hope. Group IIB 1†. See also Willey, 1904: 260-1, pl. 13 fig. 1-2a, b.
- N. larentukana Grube 1881: 110-1, as Nereis (Neanthes) Larentukana. 'Larentuka.' Group IIB 2a.
- N. limnicola (Johnson 1903: 205-22, pl. 16, 17), as Nereis limnicola, Lake Merced, California. Group IIB 1. Includes Neanthes lighti Hartman 1938: 80-2, fig. 1-4. See also Smith 1959: 349-50.
- N. macrocephala (Hansen 1882: 13-4, pl. 4, fig. 29-33), as Nereis macrocephala. Brazil. Group IIB 1.
- N. maculata Wu Boaling & Sun Ruiping 1981: 216-7 (English summary), fig. 83a-j. Canton, China. Group 11B 1⁺.
- N. mancorae. (Berkeley & Berkeley 1961: 656-7, fig. 1-4), as Nereis (Neanthes) mancorae. Peru. Group IIB 2c⁺.
- N. meggitti (Monro 1931: 580-5, fig. I-6), as Nereis (Neanthes) meggitti. Rangoon. Group IIB 1.
- N. mexicana Fauchald 1972: 70-1, pl. 11, fig. a-d. Baja California, ca. 1900 m. Group 1.
- N. mossambica (Day 1957: 77-8, 80, fig. 3e-l), as Nereis (Neanthes) mossambica. Mozambique Is. South Africa. Group IIB 2b.
- N. nanciae (Day 1949: 445, fig. 4), as Nereis nanciae. St. Helena Island. Group IIB 2a. See also Neanthes helenae.
- N. nanhaiensis Wu Boaling & Sun Ruiping 1981: 217-8 (English summary), fig. 86a-j. South China Sea. Group 11B 1⁺.
- N. noodti Hartmann-Schröder 1962: 129-30, pl. 11, fig. 65-6, pl. 12, fig. 68, pl. 20, fig. 67. Peru. Group IIB 2c.
- N. papillosa (Day 1963b: 360-2, fig. 2a-g), as Nereis (Neanthes) papillosa. W of Cape Town, South Africa. 2 745 m. Group 11A.
- N. pseudonoodti Fauchald 1977b: 27-9, fig. 7a-d. Panama. Group 11B 2c.

- N. reducta (Southern 1921: 593-5, pl. 21, fig. 7a-k, textfig. 6a-d.), as Nereis (Nereis) reducta. Chilka Lake, India. Group IIB 1.
- N. roosevelti Hartman 1939: 11-13, fig. 2c-h. Galapagos Islands. Group IIB 1.
- N. sakhalinensis (Okuda 1935: 54-7, fig. 1a-b, fig. 2a-c, fig. 3a-e), as Nereis sakhalinensis. Sakhalin 1s, Japan. Group IIB 2a.
- N. sandiagensis Fairchild 1977c: 158-60, pl. 1, fig. a-b. San Diego Trench, ca. 800 m. Group IIB 2a.
- N. seridentata Hartmann-Schröder 1959: 138-42, fig. 100-10. Gulf of Fonesca, El Salvador. Group 11B 2c.
- N. succinea (Leuckart 1847: 154-6, pl. 2, fig. 9, 11), as Nereis succinea. North Sea. Group 11B 2a. Includes Neanthes perrieri Saint-Joseph 1898: 288-92, pl. 14, fig. 69-77. See also Pettibone, 1963: 165-74, fig. 44a-e, fig. 45a-d; Day 1967: 321, fig. 14.9a-e; Imajima 1972: I08-10, fig. 32a-k, fig. 37; this study.
- N. trifasciata (Ehlers 1901b: 106-7, pl. 12, fig. 1-7), as Nereis trifasciata. Juan Fernandez South America. Group 11B 1[†].
- N. typhla (Monro 1930: 105-6, fig. 36a, b), as Nereis typhla. Off South Georgia, 245 m. Group IIB 1.
- N. unifasciata (Willey 1905: 271-2, pl. 4, fig. 85-8), as Nereis unifasciata. Gulf of Manaar, India. Group IIB 1. See also Fauvel, 1932: 93.
- N. uniseriata Hutchings & Turvey 1982: 113-6, fig. 8a-c. South Australia. Group 11B 1⁺.
- N. vaalii Kinberg I866: 171. Southern Australia. Group 11B 1. Includes Nereis albanyensis Augener, 1913: 149-53, pl. 2, fig. 6u, textfig. 14a-c. Sce also this study.
- N. verrillii (Grube 1878: 78-9, pl. 5, fig. 2), as Nereis (Lycoris) verrillii. Philippine Islands. Group 11B 2a.
- N. virens (Sars 1835: 58)*, as Nereis virens. Norway. Group IIB I[†]. See also Fauvel, 1923: 348-9, fig. 134g-k; Pettibone, 1963: 170-4, fig. 44f.
- N. vitabunda (Pflugfelder 1933: 71-2, fig. 12a-d), as Nereis vitabunda. Sumatra. Group IIB 1.
- N. willeyi (Day 1934: 39-40, fig. 6a-c), as Nereis willeyi. South Africa. Includes Nereis (Neanthes) capensis Willey 1904: 261, pl. 13, fig. 10, pl. 14, fig. 9-10 (Preoccupied). Group IIB 2a. See also Day, 1967: 320, fig. 14.8 l-p.